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Multivariate Analysis of Experimental Marine Ecosystems

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Multivariate analysis of experimental marine ecosystems

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ABSTRACT: Twelve replicate 150-l laboratory microcosms were developed using whole water samples and natural benthic communities from Narragansett Bay, Rhode Island (USA). The microcosms were scaled to the bay in terms of salinity, temperature, light input, volume pelagic community to area of benthic community, density of macrofauna, turbulent mixing, and flushing time. The microcosms were self maintaining during a six month study period with over 35 species of phytoplankton and 30 species of macro-invertebrates. Some 25 species of meroplankton entered the microcosms and successfully colonized the benthic communities. Zooplankton were present in all life stages. After an initial study of replication among the 12 tanks, the microcosms were perturbed with 3 levels of treated urban sewage for a three-month period. Three microcosms were maintained at each level with 3 tanks remaining as controls. At the end of 3 months, the sewage input was terminated and the response of the systems was followed for an additional 2 months. Both time series data and multivariate statistical analysis of over 10 different parameters indicated that the replication of the microcosms was adequate to show the effects of experimental treatments. Control microcosms were generally within the range of variation expected in Narragansett Bay. Moreover, the results suggested that the microcosms responded to the gradient of sewage input in a manner similar to that of the bay. During the two month period after the sewage was discontinued, all of the microcosms became increasingly similar, though the tanks that had been subjected to higher levels of sewage remained distinct. It was apparent throughout the study that comparisons of microcosms and natural systems must account for the large variation characteristic of each. For this, and other reasons, multivariate statistical techniques appear to provide a powerful tool for experimental ecosystem analysis.

INTRODUCTION

Ecosystem analysis – holism and reductionism

An interesting dilemma faces anyone trying to do ecosystem level research, whether it is in the marine environment or elsewhere. On one hand, there is a general acceptance that the holistic principle applies to living systems (von Bertalanffy, 1968), and that natural communities are more, or at least something other than the sum of their parts (Odum, 1971; Patten, 1971; Mann, 1972, 1975). If so, the data

gathered by traditional reductionist methods may not be very helpful in making predictive statements about the behavior of complex marine ecosystem or their probable response to perturbations of various kinds. On the other hand, natural ecosystems are usually large, unreplicated, without environmental control, and therefore protected to some degree from tampering by well meaning researchers. While it has occasionally been possible to overcome these problems in doing experimental ecosystem work on land (e. g. Likens et al., 1970; Odum, 1970), it has seldom been practical with natural marine ecosystems. As a result, our knowledge of marine ecology has developed in bits and pieces from many individual studies of the behavior and dynamics of phytoplankton, zooplankton, etc. We can only hope that the best data base that has evolved under this reductionist approach can be synthesized in some useful way through the mechanistic modeling projects now underway (Steele, 1974; Walsh, 1975; Kremer & Nixon, 1975; and numerous others).

The microcosm method

In seeking a way to carry out practical yet holistic ecosystem research, a number of workers have used small-scale living models or microcosms of larger natural systems that can be maintained and manipulated in the laboratory. The rationale and potential of the microcosm approach in general have been described by Beyers (1963) and Cooke (1971), and with specific reference to coastal marine waters by Abbott (1966). A review of the use of multi-species cultures and microcosms, especially in the marine environment, has been prepared by Levandowsky (in press). At the present time, at least five major marine microcosm studies are underway, including projects at Kiel Bay, Germany (von Bodungen et al., 1976; Smetacek et al., 1976), at Loch Ewe, Scotland (Davies et al., 1973), at Narragansett Bay, Rhode Island (Knauss et al., 1976), at Sanich Inlet, British Columbia (Takahashi et al., 1975), and at Kaneohe Bay, Hawaii (S. V. Smith, personal communication). In spite of the impressive efforts involved in these, and other microcosm studies, the methodology of microcosms (or, in some cases, mesocosms) is still evolving. For example, it is far from clear how microcosms may best be scaled to the "real world" in terms of energy inputs for biological production and physical mixing or what the effects of larger animal exclusion may be. There is also the possibility of serious artifacts from the lack of spatial heterogeneity and small size in microcosms, as well as from the "wall effects" of high surface to volume ratios characteristic of enclosed communities. As with numerical simulation models, there appears to be no generally agreed upon criteria for evaluating the credibility of living models or for comparing the behavior of microcosms with the "real" systems they represent. In a sense, microcosm research is still an iterative process in which methodological and conceptual problems of experimental design are as much a part of the study as data collection and analysis.

With these limitations and challanges in mind, however, the microcosm approach may yet prove to be a powerful tool for marine ecosystem research and management. This paper reports results from the first in a series of perturbation and recovery experiments using microcosms designed as analogs of Narragansett Bay, Rhode Island.

The experiments were designed to examine the replicability of marine microcosms, to compare the behavior of the microcosms with that of a natural marine bay, and to evaluate the use of the microcosms as a tool for studying the larger system.

METHODS

Design of the microcosms

A laboratory microcosm facility was designed to accommodate 12 plastic tanks in a flow through water bath under controlled conditions of temperature, salinity, light, flushing, physical mixing, and material input (Perez et al., 1976). During the experiment described here, an attempt was made to approximate the environmental conditions of Narragansett Bay (Table 1).

Narragansett Bay is a plankton based temperate estuary in southern New England (Fig. 1). It a well mixed system with relatively small fresh water inflow,

Table 1

Characteristics of Narragansett Bay microcosms

Volume	150 l
Depth	0.70 m
Turnover time	37 days (similar to lower Narragansett Bay, U.S.A.C.E. 1959)
Source of input water	Surface whole water samples from the lower West Passage of Narragansett Bay (Fig. 1)
Salinity	24 ‰–31.5 ‰
Temperature	6.5 C–24.2 C (maintained in a water bath to ± 1.5 C Narragansett Bay)
Photoperiod	9 to 16 hours (adjusted monthly to match the natural system)
Light energy*	21.5–31.0 ly/day
Relative turbulence	The microcosms were stirred with 0.14 m², 1.8 cm plastic mesh paddles at 32 rpm. The paddles were rotated for 30 sec., then stopped for 6 sec., then reversed for 30 sec. in a continuous cycle. The dissolving rate of hard crystalline sugar balls, our measure of relative turbulence, was – 0.150 g/min (σ = 1.005, N = 5) in the microcosms compared with – 0.174 g/min (σ = 0.004, N = 6) in the bay
Area of sediment	167 cm². Maintained in opaque box cores immersed in each microcosm. A vacuum pump system flowed microcosm water over the benthic community at 0.73 l/min, a flow fast enough to prevent the O_2 concentration over the benthos from dropping by more than 0.1 mg/l

* At surface of the tanks. Calculations of light intensity at mid-depth in the lower West Passage of Narragansett Bay during this period ranged from 14.2–21.1 ly/day (z = 5 m, K = 0.55 m⁻¹, surface light from Epply Laboratories, Newport, RI). A mixture of high intensity fluorescent and incandescent bulbs was used to give a spectral composition similar to that found at mid-depth in the bay.

generally high salinity (> 20 ‰) and little vertical stratification. The average depth is about 10 m. While there is little organic input to the bay from marshes or macrophytes, there is a clear eutrophication gradient from north to south that results from large inputs of primary and secondary sewage in the upper bay (Fig. 1). In general, however, the water quality at the location of the laboratory in the lower bay is excellent.

Experimental design

The 12 microcosms were filled in mid March, 1975, using hand bucketed water samples (to prevent damage to plankton) collected over a 6 hour flood tide from the surface of the lower West Passage of the bay (Fig. 1). For the next 7 days, the microcosms were throughly intermixed to insure a uniform distribution among the tanks. A heterotrophic benthic community was included in each microcosm in a flow

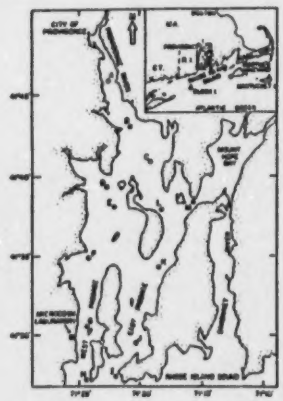

Fig. 1: Location of the microcosm laboratory on the lower West Passage of Narragansett Bay, Rhode Island (USA). The lettered stations were used to collect field data on the spatial variability of plankton and nutrients in the bay over an annual cycle in 1971—1972

through (vacuum pump) dark box immersed in the tank (Perez et al., 1976). The community used in the work discussed here was collected near the middle of Narragansett Bay in an area with unpolluted silt-clay sediments dominated numerically by the bivalve *Nucula annulata*. The sediments were screened (0.75 mm) to separate the macrofauna, which were then placed in equal numbers in each benthic box. Material scrubbed from the sides of the plastic tanks and collected on the bottom during cleaning was added to the benthos three times a week.

After the intermixing period, all 12 of the microcosms were monitored for 15 days to determine the replication of the systems. The parameters measured and methods used during this period and throughout the study are summarized in Table 2. At the end of this period, 9 of the microcosms were perturbed with 3 different levels of treated urban sewage collected from the largest treatment plant on the Providence River (Fig. 1).

Sewage inputs

Since one of the objectives of this study was to see if the behavior of the microcosms approximated that of the larger natural system, it seemed appropriate to find

Table 2

Summary of the analytical methods and sampling procedures used in this study to characterize the Narragansett Bay microcosms

Parameters	Frequency	Method
Nutrients:		
ammonia	2/week	Solorzano (1969)
nitrite & nitrate	1/week	Technicoa Autoanalyzer
phosphate	1/week	Strickland & Parsons (1968)
dissolved organic phosphorus	1/week	Menzel & Corwin (1965)
Plankton:		
chlorophyll *a*	2/week	Extracted flourescence calibrated with spectrophotometric determinations of extracted pigment (Strickland & Parsons, 1968)
ATP	2/week	Integrating photometer (Cheer et al., 1974)
Particle size frequency (0–50 μ)	2/week	Curby Assay System based on the Coulter principal
Phytoplankton	1/week	Cell counts and species identification on samples preserved in Lugol's solution
Zooplankton	1/month	Identification of major groups and counts of relative abundance in 1 liter samples
Benthos:		
macrofauna (> 0.75 mm)	initial & final samples	Identified, counted, and placed in equal numbers in each benthic box at the beginning of the experiment. On termination, each box was sieved (0.5 mm) and all animals were identified, counted, and weighed
meiofauna nematodes and ciliates	one sample only at end of sewage addition	Successive washings through 80 μm screen with mechanical disruption of detrital lumps using a needle and 12 x dissecting scope. Animals were pipetted onto a grid, counted, and major groups identified
sediment CHN analysis	final sample only	Analyzer Model 1100, Carlo Erba

out if the microcosms which resembled the "clean" lower West Passage of the bay would develop the characteristics of the more eutrophic upper regions of Narragansett Bay when they were exposed to a sewage gradient similar to that found in the natural system. Initially large quantities (4 l, 10 l and 20 l) of sewage were added to tripli-

Table 3

Composition of the treated urban sewage added to the Narragansett Bay microcosms

Nutrients	μg – at/l	Trace metals**	Dissolved μg/l	Particulate (> 0.4 μm)
NH_3 – N	367	Cd	1	—
NO_2 – N	2	Cr	1	16
NO_3 – N	94	Cu	5	28
PO_4 – P (DIP)	43	Fe	16	740
Organic – P (DOP)	37	Mn	23	6
SiO_3 – Si	82	Ni	29	22
DOC – C	2083 mg/l	Pb	2	16
		Zn	115	31
Fatty acids*	14.9 (1.5–43.1)			
Hydrocarbons*	7.8 (2.4–16.2)			

* Farrington and Quinn (1973), mean (range); samples collected from the same treatment plant as the sewage used in the experiments

** Mean of triplicate samples analyzed by Earl Davey, U. S. Environmental Protection Agency, Narragansett, R. I

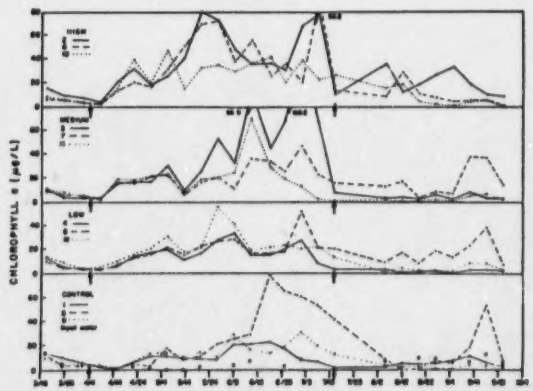

Fig. 2: Pelagic chlorophyll *a* in the experimental microcosms. Arrows indicate the beginning and the end of the sewage addition

cate microcosms to simulate an ammonia gradient from a sewage outfall of 10, 25 and 50 μg at N/l. The Providence River which has ammonia concentrations as high as 31 μg at N/l ($\bar{x}$ = 14, N = 52) and which receives 0.3 °/o sewage by volume per day provided the basis for choosing this gradient and a logarithmic series (0, 0.01, 0.1 and 1.0 °/o) of sewage by volume for new input water added three times a week. Even though the sewage addition caused only a small decrease in salinity (4.0 °/oo), fresh water was added proportionally to the lower sewage dose tanks to make the change constant for all treatments. The sewage for the entire experiment was collected at one time, analyzed (Table 3), separated into aliquots of the volume necessary to add to the bay water that was added to the tanks on three days each week (Table 1) and frozen. Later analysis of the frozen sewage showed no appreciable change in its composition over time. The sewage input was maintained for 102 days (4 April–15 July) before it was terminated and the recovery of the systems followed for the next 69 days (16 July–23 Sept.).

RESULTS AND DISCUSSION

Replication of the microcosms

For 15 days after the initial intermixing, the 12 tanks remained similar with respect to all of the parameters measured (Figs 2, 3; Table 4). Once the systems were perturbed with sewage, the tanks began to diverge and show the effect of the experimental treatment. However, replication within each treatment remained strong for another 15–20 days. At that point, one replicate in each of the treatments and in the control set began to diverge markedly with respect to ammonia (Fig. 3). The same tanks later developed extremely high nitrate and nitrite levels. It is difficult to account for this anomalous behavior with respect to nitrogen. It apparently had nothing to do

Table 4

Replication of the 12 marine microcosms just prior to the addition of urban sewage. Samples were collected 14 days after intermixing of the microcosm tanks

Parameters	Mean value	Coefficient of variation (°/o)
Nutrients (μg-at/l)		
ammonia	0.15	87
nitrate	0.20	60
nitrite	0	—
phosphate	0.07	14
dissolved organic phosphorus	0.64	8
Chl *a* (μg/l)	4.08	29
Total diatoms (cells/ml)	2547	26
Total flagellates (cells/ml)	74	93
Pelagic ATP (μg/l)	2.46	12
Suspended particles		
2.8–17.2 μm	290	15
17.2–39.0 μm	2880	15
39.0–50.0 μm	460	24
Benthic O_2 uptake (mg/m²/h)	22	12

with the sewage input, since one of the control tanks had the highest nitrogen level. Measurements of the nitrogen fluxes from the benthic boxes were not significantly higher in these tanks. Moreover, the total biomass of infauna present in the sediment (~ 250 mg dry weight) could not have provided enough nitrogen to produce the measured increases even if it had completely decomposed. The same is true of the amount of nitrogen in the pore waters of the sediments. The C/N ratio and nitrogen content of the sediments in the anomalous tanks were not significantly different from the other tanks at the end of the experiment. At this point, the source of the additional nitrogen remains unknown. Replication within treatments of the other parameters continued to be adequate to separate the effects of the various sewage levels.

Multivariate analysis of microcosm replication and response

The long, 170 day time series plots of individual parameters in the microcosms are useful in documenting the behavior of one part of the system and in analyzing the mechanisms that may operate in regulating the structure and function of the community. They also give a simple visual impression of the variation of each parameter within each treatment over time. However, one of the main reasons for using microcosms is to study the response of whole ecosystems rather than their parts. Even with the best reasonably attainable replication, the noise of measurement and sampling errors and the day to day variation of the systems themselves make it almost impossible to use the time series data alone to separate one system or microcosm from

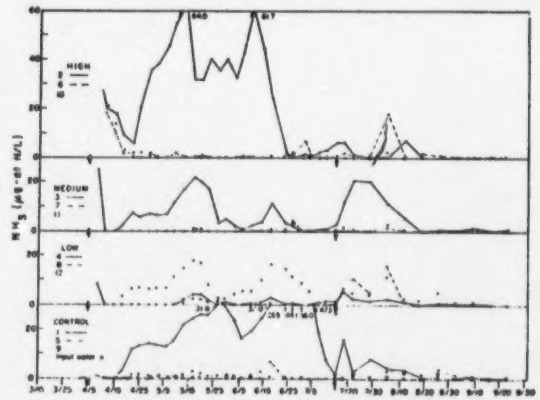

Fig. 3: Concentrations of ammonia in the experimental microcosms

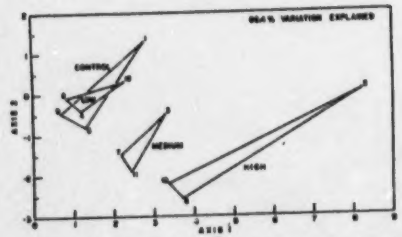

Fig. 4: Canonical variates analysis of pelagic chlorophyll *a*, diatoms, flagellates, pelagic ATP, suspended particles (2.8 μm, 15.2 μm, 39 μm) and ammonia in the experimental microcosms during the first month with sewage input. The lines connect replicates within each treatment. The numbers refer to individual microcosms

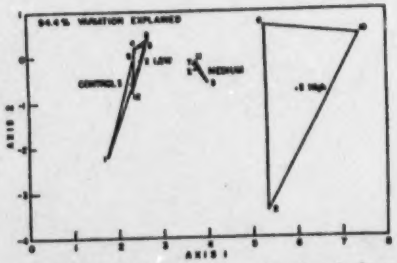

Fig. 5: Canonical variates analysis of chlorophyll *a* and nutrients in the experimental microcosms during the three month sewage addition. The mean position of each treatment level is shown along with the individual means of each treatment

another or to separate one system in its present state from itself at some other state. Analyses are needed which incorporate a number of parameters simultaneously in arriving at an objective statistical description of ecosystem state or conditions. Our feeling is that a number of multivariate statistical techniques, including canonical variate analysis (Blackith & Reyment, 1971) and correspondence analysis (David et al., 1973) are especially appropriate for use with experimental ecosystem studies that produce large amounts of data on a large number of parameters. The application of these techniques to ecological data from natural systems has already been described (Chardy et al., 1976).

The relative variation within and among treatments in the microcosms during the first 30 days after sewage additions were begun is clearly evident in a canonical variates analysis of a data set that included ammonia, chlorophyll *a*, numbers of diatoms, numbers of flagellates, pelagic ATP, and the numbers of particles in three

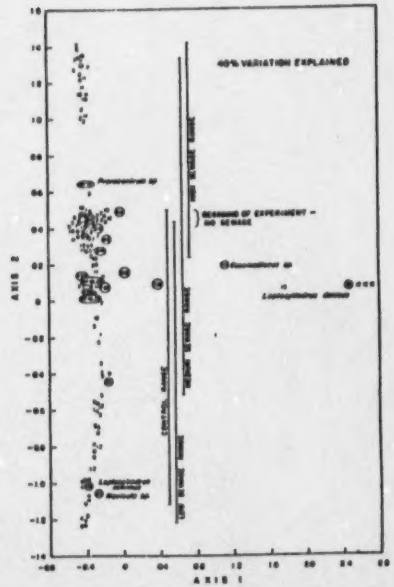

Fig. 6: Correspondence analysis of data on the species composition and abundance of the phytoplankton in the experimental microcosms during the three month addition. Numbers represent samples in individual microcosms while the letters represent particular species of diatoms (D) or dinoflagellates (DF) or flagellates (F) that were associated with the various samples. All of the tanks were similar at the beginning of the experiment before sewage was added (see Fig. 4 for numbers of individual microcosms)

size ranges (Fig. 4). The outlying point in each of the replication triangles represents the individual microcosm in each treatment that developed the anomalous ammonia values discussed earlier. Since the tanks with high nitrogen levels did not appear to differ with respect to any of the other parameters (Fig. 2), it is evident that the multivariate analysis will reflect the extreme behavior of any one parameter. A similar canonical variates analysis on a data set that included all of the nutrients and chlorophyll *a* from the entire three month period during which the sewage inputs were maintained again showed that the replication remained adequate to show treatment effects along axis one and anomalous ammonia values along axis 2 (Fig. 5).

The data used in canonical variates analysis came from relatively aggregated parameters such as total chlorophyll *a*. Since the treatments could easily be separated

at this level, it was somewhat surprising to find that variations in the more detailed measurements of phytoplankton species abundance prevented a clear separation of treatment on the basis of the total phytoplankton community structure or on the basis

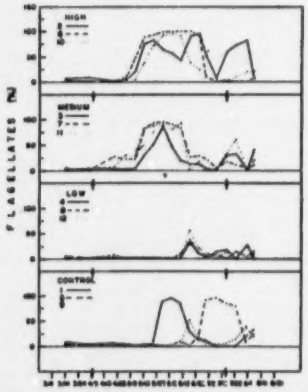

Fig. 7: Contribution of flagellates to the total phytoplankton in the experimental microcosms. Narragansett Bay typically shows a shift from diatoms to flagellates in the summer flora

of "characteristic species" (Fig. 6). The correspondence analysis of taxonomic data did clearly show initial similarity of all of the microcosms. It also reflected some tendency for flagellate groups, especially *Prorocentrum*, to be more abundant in the higher sewage treatments (Figs. 6 and 7). However, the results suggest that the large amount of effort involved in the taxonomic analysis at lower trophic levels did not provide data that were particularly sensitive to perturbations of this kind. It is not clear whether this result comes about because individual species are relatively insensitive to the perturbation or because the large amount of variation inherent in less aggregated data, including the seasonal change from diatoms to flagellates, makes it more difficult to measure the response of individual species in the context of a total plankton community.

Comparison with the natural system

One of the prevailing myths in marine ecology is that the goal of microcosm studies is to develop an exact replica in miniature of some particular natural system. Such a goal is neither attainable or necessary. What is desired, however, is to develop a microcosm which is generally similar to the larger system in terms of its trophic structure, the major features of its taxonomic composition, its level of productivity, its rates of material cycling, and in its response to perturbations. The microcosm

community should also be self-maintaining over a time span that is appropriate for the processes being studied. It is probable that neither the microcosms described here nor those of any other study yet reported have fulfilled all of these criteria. It is hard to know this for sure since, as mentioned earlier, there is no generally agreed upon

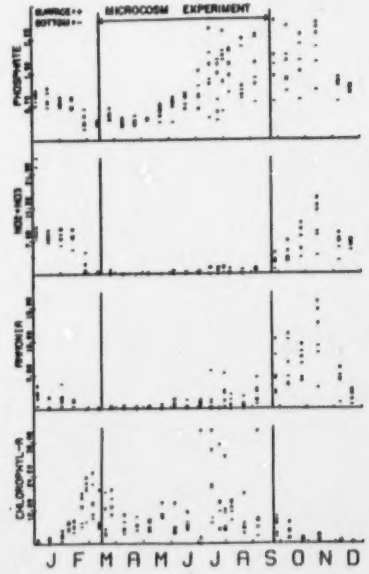

Fig. 8: Range of chlorophyll *a* and ammonia values found in biweekly samples of surface and bottom water at stations F, G, H in the lower West Passage of Narragansett Bay from August 1971–August 1972 (Fig. 1). The period of microcosm study in 1975 is shown for reference

criteria for the success of microcosms with respect to any of these goals. Nor is it clear that any one of them is of greater or lesser importance than the others for any particular study. It is clear, however, that comparisons of microcosms and natural systems must consider the variation of each. For example, if one compares the time series data from the control microcosms in this study with measurements of the input water collected from the laboratory dock, it appears that there were often appreciable differences (e.g. Figs 2 and 3). However, there is no one chlorophyll or nutrient value for Narragansett Bay. Instead, there is a range of values that one might normally expect

to find in different parts of the bay at different times of the year (Fig. 8), and it is against this background of natural variation that the behavior of the microcosm should be evaluated. With the exception of the anomalously high nitrogen levels in one tank, the control microcosms generally fell within the range of values characteristic of the lower West Passage of Narragansett Bay. A canonical variates analysis of nutrient and chlorophyll data from the microcosms and from 13 stations located throughout the bay confirmed this intuitive analysis and indicated that the microcosms responded to sewage inputs by developing characteristics similar to those found along a gradient from the Providence River to the mouth of Narragansett Bay (Fig. 9).

The microcosms remained throughout the study as plankton based systems with grazing food chains containing over 30 forms of phytoplankton and zooplankton. The benthic communities contained a healthy assemblage of macrofauna similar to that

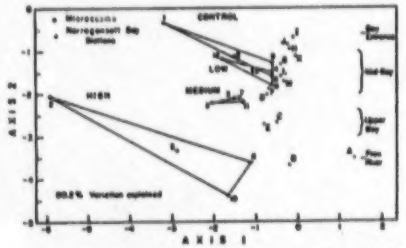

Fig. 9: Canonical variates analysis of chlorophyll and nutrient data from the experimental microcosms and for the same parameters from an annual field study of surface and bottom water at 13 stations in Narragansett Bay. Location of the field stations is shown in Figure 1. Axis 1 portrays the anomalous microcosms, whereas axis 2 gives the eutrophication gradient in the bay and in the microcosms. Over 90 % of all the sewage input to the bay enters in the Providence River. The resulting marked gradient down the bay resembles the gradient developed among the microcosms as a function of sewage input

found in Narragansett Bay. While the benthos was composed of 10 species of macro invertebrates at the beginning of the experiment, the diversity increased through the natural seeding of meroplankton in the input water to 35 species by the end of the study. Benthic biomass increased from 2–4 fold and measurements of oxygen uptake and ammonia flux from the sediment indicated that total benthic metabolism was similar to that found in the bay (Nixon et al., 1976).

Effect of sewage inputs

The addition of sewage to the microcosms brought about an immediate increase in inorganic and organic nutrients (Fig. 3) which was followed by clear increases in chlorophyll, particulate ATP, suspended particles and cell numbers (Fig. 2). In general, the time series data show higher values and greater variation for all these

Table 5
Composition and metabolism of the benthic community in the experimental microcosms from mid – March to mid – September. Sewage inputs were maintained from April through mid – July

Components	Control	Low	Treatment (volume of sewage) Medium	High
Macrofauna (total community)				
number of species (initial)*	10	10	10	10
(final)**	16	14	16	13
biomass increase (mg dry)	936 ± 216	817 ± 383	559 ± 158	724 ± 428
Meiofauna (8 mm core)				
number of ciliates	9.0 ± 4.4	12.7 ± 11.6	16.0 ± 10.6	105 ± 137
number of nematodes***	21.3 ± 8.6	69.3 ± 28.7	80.3 ± 34.3	43.7 ± 20.5
(at the end of sewage additions)				
Total benthic oxygen uptake during the experiment (gm)	3.62 ± 0.84	2.67 ± 0.34	3.71 ± 0.29	4.39 ± 0.43
Sediment carbon in the top 1 cm at the end of sewage addition (mg/gm)	24.86 ± 10.37	21.84 ± 3.63	22.73 ± 6.63	36.87 ± 12.86
Sediment nitrogen in the top 1 cm at the end of sewage addition (mg/gm)	3.03 ± 1.46	2.82 ± 0.58	2.94 ± 0.94	5.23 ± 1.9
Sediment C:N ratio	8.20	7.74	7.73	7.05

* Most abundant species were *Ampelisca abdita*, *Nucula annulata* and *Malinia lateralis*
** Most abundant species in all treatments were *Nucula annulata*, *Tharyx acutus*, and *Polydora ligni*
*** Major genera were *Terschellingia*, *Odontophora*, and *Sabatieria*

parameters in the microcosms with higher sewage input. There was also a tendency for the phytoplankton in the sewage tanks to contain a larger percentage of flagellates (Fig. 7). However, as shown in Figure 6, changes in the specific taxonomic composition and relative abundance of the plankton as a result of the sewage addition could not be demonstrated with correspondence analysis. The same was true for the taxonomic composition, growth and metabolism of the benthos, where the only statistically significant change appeared to be an increase in the carbon and nitrogen content of the surface sediments in the high sewage microcosms (Table 5).

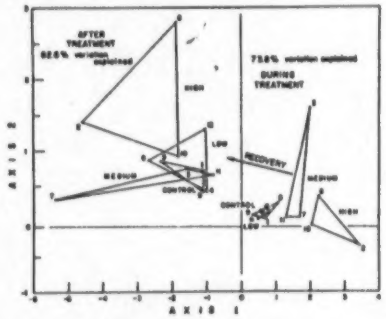

Fig. 10: Canonical variates analysis of chlorophyll *a*, nutrients, pelagic ATP, and particle counts in the experimental microcosms during three months with sewage input compared with the same analysis during the two months following termination of the sewage input. Substantial recovery of lower treatment levels is apparent in overlap of the replication triangles

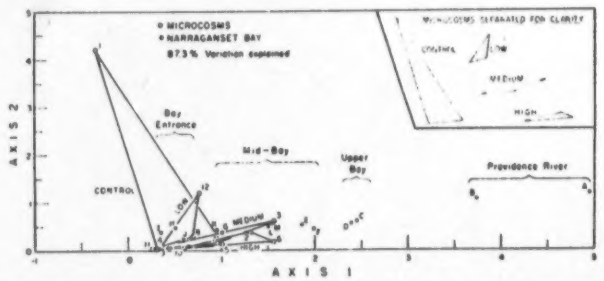

Fig. 11: Canonical variates analysis of chlorophyll, ammonia, nitrate, and nitrite in the microcosms and in Narragansett Bay during the recovery period. Good agreement with lower bay stations is indicated by all treatment levels for this data set

Recovery

The time series data show declines in cell counts, chlorophyll, and pelagic ATP that began before the sewage was stopped (Fig. 2). Marked fluctuations in these, and other parameters became particularly apparent and are also characteristic of Narragansett Bay in the warmer months. The high seasonal variability obscures clear trends in the single parameter time series data. However, canonical variates analysis of nutrient values, chlorophyll *a*, pelagic ATP, and particle counts during the three month sewage addition and the two month recovery period did show differences between the sampling periods (Fig. 10). After the sewage was stopped, the replication triangles all began to overlap to some degree, even though seasonal changes had influenced the general condition and variability of all the microcosms. A reduced data set from the microcosms which included chlorophyll, ammonia, nitrate and nitrite was compared with the 13 bay stations during the recovery period using canonical variates analysis (Fig. 11). All treatment microcosms and two controls overlap mid and lower bay stations indicating good recovery for these parameters. Control microcosm 1, by contrast, was positioned high on Axis 2 due to very high values of nitrate and nitrite, apparently derived from earlier high ammonia values. Recovery of the microcosms that had been subjected to the high sewage inputs was still far from complete with respect to all parameters, even though the recovery period was almost twice as long as the flushing time of the systems.

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Ecological studies on the deep-water pelagic community of Korsfjorden (western Norway)

The search for a trophic pattern

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ABSTRACT: As part of a project aimed at assessing the available energy in a pelagic system and the efficiency of its transfer, monthly biomass estimates of the 23 main macroplanktonic and mesoplanktonic species have been made in Korsfjorden (Norway). Sampling was carried out over approximately 3 years (1971–1974) and results are presented as mg dry weight in a 690 m² water column. The total annual stocks of the various species were not constant in the 3 years of sampling. Principal components analyses of the monthly stocks in each of the 3 years show striking differences in the correlation matrices from year to year. On the basis of known and supposed feeding habits, the species have been classified as herbivores, omnivores, or carnivores. The monthly biomass estimates of these groups show a consistent pattern from year to year. This, in contrast to the variable correlations between individual species, indicates that there can be considerable flexibility in the specific composition of a planktonic community without correspondingly marked effects on its trophic structure.

INTRODUCTION

One of the major problems in studies of pelagic productivity concerns the availability of energy and the efficiency of its transfer within the community. In view of the dominance of *Calanus* species in many temperate areas where advanced plankton studies have been carried out, one is tempted to treat total zooplankton as being synonymous with secondary production, i.e. as being composed exclusively of herbivores providing the necessary link between primary producers and the nektonic and benthonic carnivores. Many planktonic communities, however, have a considerable carnivorous component which must surely involve much cycling of organic material within the community and reduce the energy available to dependent communities.

Examples of this type of community are found in the depths of Norwegian fjords, well below the euphotic zone. The proximity of Korsfjorden to the Biological Station, University of Bergen, led to the choice of this site for elucidating the trophic dynamics of a community, as represented by the stock present in a water column 1 m² in cross-section. The fjord has a complicated topography. The main basin is 690 m deep and the offshore sill lies at approximately 250 m. Around Korsfjorden are numerous